

The University of Chicago

THE RELATIVE EFFECT OF A
CEREBRAL LESION UPON LEARNING,
RETENTION AND TRANSFER

A DISSERTATION SUBMITTED TO THE FACULTY
OF THE DIVISION OF THE BIOLOGICAL SCIENCES
IN CANDIDACY FOR THE DEGREE OF DOCTOR OF
PHILOSOPHY

DEPARTMENT OF PSYCHOLOGY

1938

By
STANFORD C. ERICKSEN

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THE RELATIVE EFFECT OF A CEREBRAL LESION UPON LEARNING, RETENTION, AND TRANSFER

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INTRODUCTION

This experiment was designed to test the relative effect of a cerebral lesion of a given size and locus upon learning, retention, and transfer. We ran three groups of normal rats in three situations that are universally accepted as being tests of learning, retention, and transfer. Three other groups were subjected to a lesion of approximately the same size and locus, and they were then tested in the same situations. The question is: does the lesion exert a differential effect in the three test situations?

The experimental arrangement is schematized in table 1. The effect of the lesion on the initial learning of maze B is derived from a comparison of the records of groups I and II. A comparison of the data for groups III and IV gives the effect of the lesion on the relearning of maze A, and the data on transfer are obtained by comparing the records of groups V and VI.

The effects of lesions upon learning and retention have been extensively investigated, but there has been no comparison of the *relative* effect of a lesion of a given size and locus upon the two processes, with the exception of two studies.

Lashley (2) introduced the lesion prior to learning and then compared its direct effects upon learning with its indirect effects upon subsequent relearning. Lashley's method has been crit-

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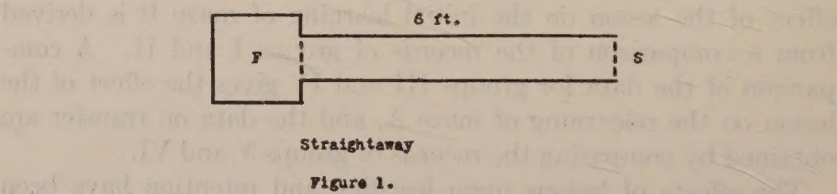
The writer gratefully acknowledges the assistance of Professor Harvey A. Carr throughout the course of this investigation. Appreciation is also extended to Dr. I. Krechevsky for his help and training in the experimental techniques used.

icized by Melton (7). We avoided this criticism by inserting the lesion prior to both learning and relearning. Cameron (1) also obtained data when the lesion was inserted prior to learning and prior to the test for retention. His comparison, however, is based upon the records of only nine animals per group, and his retention test is complicated by the fact that the rats learned two maze patterns prior to learning the pattern for which retention was tested.

Cameron's study is the only one that has dealt specifically with transfer. However, he did not insert the operation prior to the

TABLE 1
Experimental arrangement

GROUP	NUMBER OF RATS	SEQUENCE OF EVENTS
I	36	learn B
II	45	Operate.....21 days.....learn B
III	27	Learn A.....21 days.....relearn A
IV	31	Learn A, operate. 21 days.....relearn A
V	29	Learn A.....21 days.....learn B
VI	39	Learn A, operate. 21 days.....learn B



transfer test, as in our experiment. The same objection applies to Cameron's study of transfer as to Lashley's study of retention in that he studied the indirect effects on transfer of a lesion that was inserted prior to learning or prior to retention.

Before beginning the above experimental cycle, all the animals were given a preliminary seven-day period of training in a straight-away maze represented in figure 1. This was done to eliminate fear and curiosity in a novel situation, and to accustom them to react to the food situation. With all six groups this preliminary training immediately preceded the introduction to

the maze. The effectiveness of this training is attested by the fact that all of the normal animals completed the first learning trial in less than five minutes. The daily procedure of this preliminary training period is described in table 2.

Only male rats of the hooded variety were used in the experiment. They were taken from the regular Chicago stock, and all were between ninety and one hundred days of age at the time of starting the preliminary training.

It is desirable that all six groups, and especially the members of

TABLE 2
Preliminary training schedule

DAY	CHARACTER OF TRAINING
1	30 minutes in straightaway. Free to explore and eat. Three rats at a time
2	20 minutes. Same procedure
3	15 minutes. Same procedure
4-7	One rat at a time. Three trials per day. First trial—one minute feeding. Second trial—one minute feeding. Third trial—three minutes' feeding

TABLE 3
Learning records for maze A

GROUP	N	TRIALS	ERRORS
III	27	21.6	64
IV	31	20.2	56
V	29	21.0	61
VI	39	22.5	62

the compared groups, should be approximately equal in learning ability. The method of chance selection was employed to achieve this result. The equality attained can be tested for groups III-VI inasmuch as all learned maze A as normal animals as the initial step of the experimental cycle. The learning data for this comparison are given in table 3. These are mean scores. Comparable time records were not obtained for some of these animals.

The maximum differences are within the range of chance error. Presumably groups I and II are also equally well equated. It

will be noted that the operated group IV made slightly better scores than the other groups. Some of these animals were the last to be trained, and it is possible that they may have profited slightly from an improvement in the experimenter's technique in handling the animals.

Two 12-unit multiple-T mazes of different pattern were used. They are shown in figure 2. This type of maze was selected for several reasons. It has been widely used. It is said to possess a high degree of reliability. Because of its complexity, it should

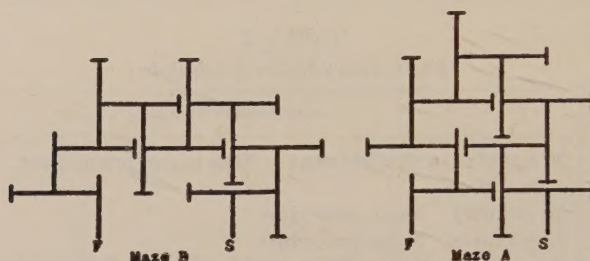


FIG. 2

TABLE 4
Percentages of transfer with normal animals

GROUP	N	TRIALS	ERRORS	TIME
				<i>seconds</i>
I	36	19.75	53.05	877
V	29	9.9	19.62	305
Per cent of transfer.....		50	63	65

be sensitive to the effects of the lesion. The pattern of maze A is the one used by Leeper (4) with the thirteen drop-doors to prevent retracing. The pattern of maze B was designed so that it would mediate a medium amount of positive transfer with normal animals, and so that the two mazes would be approximately equal in difficulty. The pattern finally adopted was selected on the basis of a considerable amount of preliminary experimentation. The empirical data justified our expectations in both respects. The amount of transfer is shown in table 4.

The learning records for the two mazes are nearly alike, as may be seen from an inspection of table 5. The data from maze A are based upon the combined records of groups III-VI consisting of 126 animals. Inasmuch as the two groups are presumably equal in ability, it appears that maze A is slightly more difficult though the difference is not great.

Lashley's operative technique, and method of brain reconstruction and measurement were employed. The operations were performed under deep anaesthesia by thermocautery. Aseptic methods were employed, and no infections were observed when the brains were removed, stained, and sectioned. Only six animals failed to recover from the effect of the operation. The operations on groups IV and VI, the operated relearning and operated transfer groups, were performed the third day after they had met the criterion. This two-day delay was used to

TABLE 5
Learning records for mazes A and B

GROUP	N	TRIALS	ERRORS
III-VI	126	21.6	60.8
I	36	19.75	53.0

permit the animals to regain to some extent their normal strength after the meager diet in the maze situation. This left a 17-day recovery period before they resumed training. Approximately the same time was allowed between operating and learning with the animals in group II.

The special effect, if any, of subcortical injuries was not taken into account. In nearly every case some parts of the thalamic or archiopallium structures were destroyed between levels 12 and 18 of Lashley's rat-brain maps. Lashley (2), Lashley and Wiley (3), and Maier (5) have all checked for possible effects from subcortical injuries and have not found these to be differentiating factors in maze learning.

The retarding effect of a lesion on a maze habit is known to vary with its size. The retarding effect of a lesion of a given size probably varies with the complexity of the maze pattern. Inas-

much as there are no data on the effects of lesion size on the multiple-T maze patterns used, our first problem was the selection of a lesion size that would give a medium amount of retardation. The size was determined on the basis of some preliminary experimentation. Six rats were subjected to an approximately 25 per cent lesion, and all failed to make any progress in learning maze B. Six animals were then subjected to an approximately 13 per cent lesion, and only one rat exhibited any retardation in learning, as compared with normal animals. Obviously the first size was too large, and the second too small for our purposes. Consequently we arbitrarily selected a lesion of approximately 19 per cent.

Naturally it was impossible to produce lesions of exactly the

TABLE 6
Size of lesion in percentage terms

GROUP	MEAN AND STANDARD ERROR	MINIMUM	MAXIMUM
		<i>per cent</i>	<i>per cent</i>
II	18.53 $\pm$ 0.32	14.2	24.2
IV	18.68 $\pm$ 0.40	14.1	22.5
VI	19.08 $\pm$ 0.42	14.0	24.9

same size for all of the individual animals. However, our problem only requires that the three operated groups be approximately equated in respect to size of lesion. The comparative data on lesion size are given in table 6.

As may be seen, the average size and distribution of the lesions are approximately the same for the three groups. The difference between the means and the range of variation within the groups are as small as could be expected.

Previous experiments have shown that the retarding effect of a cerebral lesion upon a maze habit does not vary with its location. Consequently the locus was arbitrarily selected on the basis of its accessibility and consistent landmarks on the skull. While an equation of the groups in respect to locus is not essential for the purposes of our experiment, yet it is desirable, and consequently

the attempt was made to keep the locus as constant as possible for all of the animals.

The diagrams in figure 3 show representative lesions from each of the three operated groups. They are presented merely to show the typical range of variation in size and locus. Any quantitative measure of variation in locus would have been extremely difficult and would be of little value in the present experiment. The shape of the lesion was approximately uniform for all of the animals.

The following procedure was used in running the rats. Two trials were given daily. About half of the rats were run in the forenoon, the rest in the afternoon. The time of day was con-

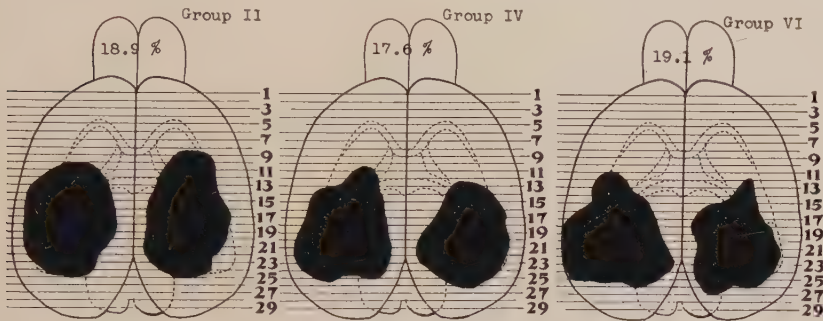


FIG. 3

stant for each animal. No consistent diurnal variations were observed. During most of the experimental period, some animals from each of the six groups were trained in the maze on any given day.

Only a 30 second feeding period was allowed between the first and second trials. After the second trial five minutes of feeding time was allowed. Many of the operated animals were cut to four and one-half minutes in the final eating period as they were much more rapid eaters. Bread soaked in warm milk was the only food used when the rats were learning the mazes.

The interval between initial learning and the relearning and transfer tests was 21 days. This was selected in order to secure a medium amount of forgetting for the normal animals. On the

20th day the rats were given three preliminary trials in the straightaway; on the 21st day they were again introduced into either maze A or B.

An error was counted only when the rat entered a blind alley the full length of his body. Time was kept from the moment the rat made the first turn out of the starting box until his nose appeared in the food box. The criterion of mastery was two out of three errorless runs with no more than one error on the third trials, such as: 0, 1, 0, or 0, 0, 1, or 1, 0, 0.

TABLE 7
Comparative data of effect of lesion on normal and operated rats

GROUP	N LEARN	N FAIL	TRIALS	ERRORS	TIME
A. Learning of maze B					
I—normal.....	36	0	19.75	53.0	877
II—operated.....	26	19 (42 per cent)	20.5	52.5	1,005
B. Retention of maze A					
III—normal.....	27	0	5.4	4.3	115
IV—operated.....	26	5 (16 per cent)	8.57	16.4	332
C. Transfer to maze B					
V—normal.....	29	0	9.9	19.6	305
VI—operated.....	28	11 (28 per cent)	15.6	34.6	498

EXPERIMENTAL RESULTS

The comparative data on the effect of the cerebral lesions on learning, retention, and transfer are given in table 7. This lists for each group the number of successes and failures and the mean trial, error, and time scores for the successful animals.

A. Failures

The first important fact is the difference between the normal and the operated groups in respect to failure to learn. There were no failures in the three normal groups, but a considerable

number of failures in each of the operated groups. Under the conditions of our experiment a lesion is evidently responsible for a certain proportion of failures. The failures were those animals that failed to meet the criterion of mastery within an arbitrary limit of trials. This limit was 100 trials for the learners, and 75 trials for the relearners and transfers.

The percentage of failures varies with the task. This is shown in table 7. Initial learning gave the greatest proportion and retention the least, while transfer was intermediate. It may be noted that the three tasks may be ranked in respect to novelty in the order of: learning, transfer, and relearning. This is the same ranking as we have for difficulty of task if the trials to learn by normal animals are used as the criterion of difficulty. The percentage of failures due to the lesion thus varies directly with the novelty and the difficulty of the task.

The splitting of the groups into either learners or failures appears to be an "all or none" phenomenon. This condition is illustrated in figure 4. These graphs are interpreted as follows: the solid line marked "failure" represents the learning curve of the rat with the best record among the failures, and the dashed line marked "success" represents the learning curve for the poorest animal in the successful group. These two animals, then, represent the least difference in performance between the success and failure groups. The lines marked with an "x" are the average curves for the two groups.

Examination of these learning curves in figure 4 shows that the separation between the learners and the failures is most marked with the initial learning group, group II. The separation is still apparent in the relearning group, IV, though in this case there is some overlapping. With the transfer animals, group VI, the separation is again complete.

These data are significant in that they indicate the presence of a distinct qualitative difference in learning ability in all three of the conditions of this experiment. In effect, this "all or none" phenomenon is the same as that described by Maier (5 and 6) in his "reasoning" tests with rats. In his own experiments this splitting of the groups into "passed" or "failed" occurred in the

reasoning test but not in maze learning. Nor does he find this effect in the maze performance of operated animals as reported

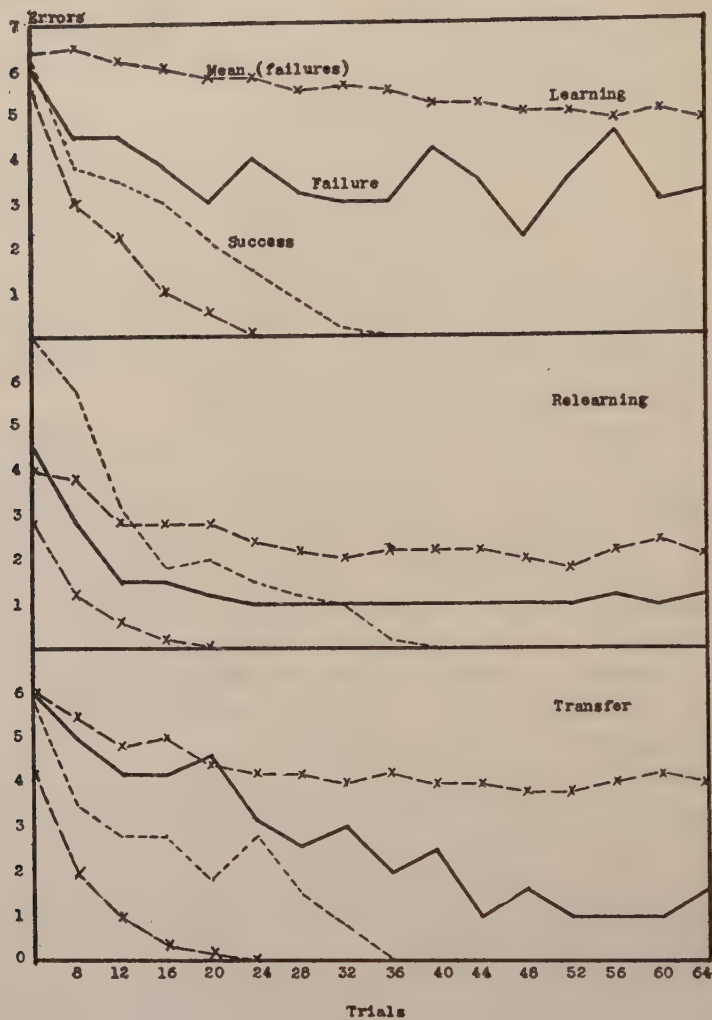


FIG. 4

by Lashley (2), or Lashley and Wiley (3). Of course, it is frequently observed in most lesion studies that some of the operated animals fail to learn the problem. This is usually explained as

being the result of an excessively large lesion or as due to some unknown chance or individual effect. Apparently the "all or none" effect of the lesion on learning in the present experiment is due to the complexity of our maze patterns. Our data disprove Maier's conclusion that maze learning, and what he terms "reasoning," necessarily represent two different kinds of mental operation in that a cerebral lesion affects them differently in respect to the presence of failures.

Presumably the composition of the failure group is not a matter of chance. There must be some explanation of the fact that certain rats failed while others did not. Two hypotheses may be advanced whose truth can be subjected to an empirical test.

1. *Learning ability.* The first hypothesis is that the susceptibility or immunity of a rat to failure following a cerebral lesion is to some extent a function of its learning ability—that the successful rats were the better learners, while the failures were the naturally poorer learners. This hypothesis can be tested with groups IV and VI, because they both learned maze A before the operation and the subsequent testing for retention and transfer. To what extent did those rats that made poor records in learning maze A tend to fail on the subsequent retention and transfer tests? The learning data on Maze A (as normal animals) of the successes and failures in the retention and transfer tests are given in table 8.

From these tables it can be seen that there is a marked difference in the initial learning ability of these two groups. Evidently the "success" or "failure" effect of a cerebral lesion of this type is to a considerable extent a function of the learning ability of the rat. The poorest learners are handicapped the most.

This hypothesis cannot be empirically tested for group II as these rats were not subjected to a learning test prior to the operation. Inasmuch as the rate of learning functions as a selective factor in groups IV and VI, we may legitimately assume that its influence was also present in group II.

Inasmuch as the percentage of animals affected varied directly with the difficulty of the task, we may thus conclude with some degree of probability, that the effect of the lesion varies directly

with the novelty or difficulty of the task and inversely with rate of learning.

2. *Size of lesion.* This is the second factor which may determine the success or failure of the rat in the maze. It can be seen in table 6 that the size of the lesion varied within certain small limits from rat to rat within each group. Previous experiments have thoroughly established the fact that the retarding effect of a lesion on learning and retention varies directly with its size. We thus have the possibility that the division of the rats into successes and failures is partly a function of chance differences in

TABLE 8
Comparison of the successes and failures as to initial learning ability as normal animals

	NUMBER OF ANIMALS	TRIALS	ERROES
A. Retention (group IV)			
Successes.....	26	19.15	52.8
Failures.....	5	25.6	74.2
Difference.....		6.45	21.4
B. Transfer (group VI)			
Successes.....	28	20.2	51.5
Failures.....	11	28.5	88.45
Difference.....		8.3	36.95

size of lesion. There are three sets of facts that are relevant to this second hypothesis.

a. For the successful animals, we correlated the size of the lesion with their subsequent records in the learning, retention, and transfer tests. These data are given in table 9. These are product-moment correlations.

All these correlations are small, but also the variations in size of lesion are small in magnitude. If the lesions had been constant in size, these correlations would have been zero, as the correlation of a variable with a constant is zero. The data show that the small variations in size of lesion do affect to some slight degree

the number of trials and errors made by the successful animals in adjusting to the initial learning situation. The correlations are negligible in the relearning and transfer situations.

b. Reference may be made to the data of our preliminary tests. With a 25 per cent lesion all six rats were failures. With a 13 per cent lesion only one rat was slightly retarded; the other five learned as quickly as the normals. Evidently success or failure is a function of variations in size from 13 to 25 per cent. It can be noted in table 10 that the range of lesion size in nearly all the groups approximated these limits.

The facts of these preliminary experiments give some indications which lead to the *concept of critical size*. It has generally been assumed that degree of retardation in a maze varies quantitatively with size of lesion up to as high as 60 per cent of the entire

TABLE 9
Correlations between lesion size and learning scores

GROUP	TRIALS	ERRORS
II—learn.....	0.27	0.27
III—retention.....	0.07	0.02
IV—transfer.....	0.15	0.11

cortical area. This relation was thought to be linear by Lashley (2). Lashley and Wiley (3) found data on this problem and presented a logarithmic curve. The present data suggests still a different relation. There appears to be two critical sizes of brain lesion. As one passes by the first we go from no retardation to retardation of various degrees. In passing by the second critical size, we pass from retardation to failure. Our data indicate that the upper critical point lies somewhere between 20 and 25 per cent. Perhaps the existence of this upper limit is a function of our complex maze pattern. The particular value it might have for any given rat is certainly, to some extent, a function of the learning ability of that rat.

c. We computed the mean size of the lesion for the successes and the failures in each of the three operated groups. These values and the maximum range of variation are given in table 10.

The mean size and the maximal range of the failures are slightly greater than the corresponding values for the successes in groups II and IV. The mean size for all of the failures is also a little larger than for the successful animals. These data indicate that a slightly greater proportion of the large sized lesions is to be found among the failures.

The distribution of the lesions in respect to size for the successes and failures is plotted in figure 5. The number of animals in these two groups differs materially. Hence the relative number of the various sized lesions must be measured in percentage terms, and it is these percentage values that are plotted in figure 5. The height of the solid lines denotes the various percentage values

TABLE 10
Lesion size of successes and failures

GROUP	N	PER CENT SUCCESSES		N	PER CENT FAILURES	
		Lesion	Range		Lesion	Range
II—learn.....	26	18.1	14-22	19	19.1	14-24
IV—retention.....	26	18.6	14-22	5	18.8	14-22
VI—transfer.....	28	18.7	14-24	11	20.0	17-24
Average size.....	80	18.5		35	19.36	

for the successful animals, and the cross-hatched lines for the failures. A greater proportion of the 20-24 per cent lesions is found in the failure group, with a corresponding smaller proportion of the smaller lesions.

Our preliminary tests indicated that failure is to some extent a function of size of lesion. It is thus possible that these small differences in size of lesion may have operated as a selective factor. The influence of such a factor, however, must have been slight, and the differentiation of our rats into successes and failures must be accounted for in the main in terms of other selective conditions. Learning ability has been shown to be operative, but it is hardly probable that the differential results can be explained entirely in these terms. Presumably other selective

factors were present, but we shall refrain from any speculation concerning their nature.

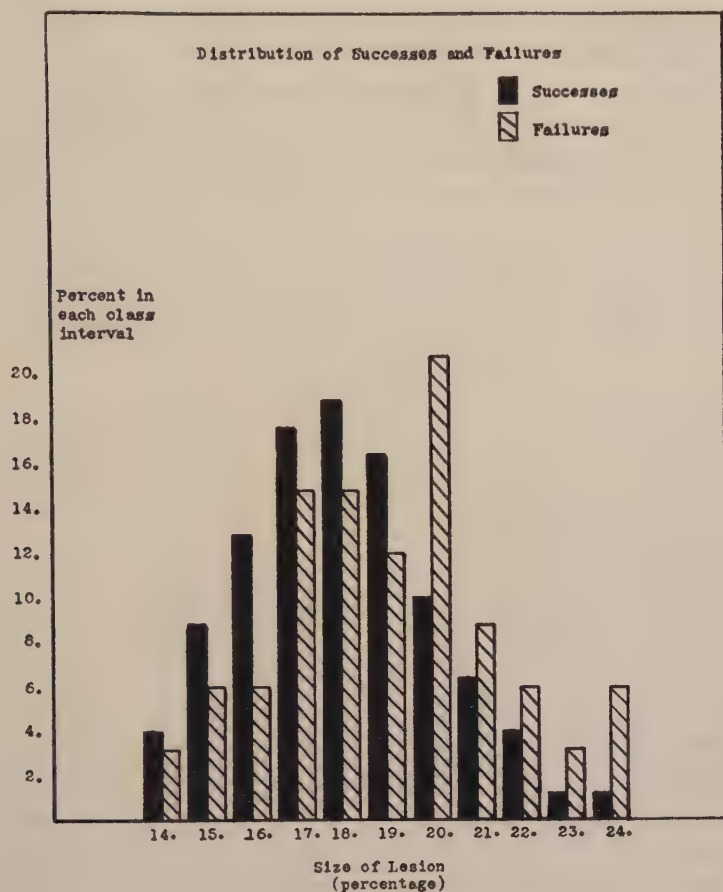


FIG. 5

B. Successful rats

A comparison of the data in table 7 is illegitimate, for the operated animals represent groups that have been selected to a considerable extent on the basis of rate of learning. The success groups are superior to the normal groups in respect to average

learning ability, and they thus may be expected to make relatively better records in the three test situations.

All comparisons must make allowance for this selective factor. The successful operated rats can be roughly equated with their corresponding normal group by the following procedure: Discard from group I a number of the poorest animals equal to the number of failures in group II. The same procedure is followed for the other two conditions except that we discard from the normal groups animals that are matched with the failures in respect to

TABLE 11
Comparison of the successful operated animals with a select group of normals

GROUP	N	TRIALS	ERRORS	TIME
A. Learning maze B				
I—normal 36-19.....	17	14	39.1	712
II—operate.....	36	20.5	52.5	1,005
Difference.....		5.5	13.4	293
B. Relearning maze A				
III—normal 27-5.....	22	3.9	3.3	83
IV—operated.....	26	8.6	16.4	332
Difference.....		4.7	13.1	249
C. Transfer from maze A to B				
V—normal 29-11.....	18	8.3	17.0	272
VI—operated.....	28	15.6	34.6	498
Difference.....		7.3	17.6	228

their previous learning records on maze A. Table 11 gives this new data. By dividing the differences given in this table by the score of the corresponding normal group, we obtain the percentages of retardation for each test situation. These measures of amount of retardation due to the lesion are given in table 12.

By all three criteria, the lesion exerted the greatest retardation upon retention and the least upon learning, with transfer occupying an intermediate position. The amount of retardation thus varies inversely with the novelty and the difficulty of the task.

Our previous data have shown that the number of failures varies directly with the difficulty of the task. We are thus confronted with the apparent paradox that the effect of the lesion varies directly with the difficulty of the task when measured in terms of number of failures, while it varies inversely with difficulty when measured in terms of its retarding effect upon the successful animals.

Two facts are relevant to an understanding of this inverse relation between degree of retardation and difficulty of the task (table 12): (1) The three pairs of groups were subjected to unequal degrees of selection. Nineteen of the poorer animals were eliminated from the learning groups, 11 from the transfer groups, and only 5 from the retention groups. The amount of selection,

TABLE 12
*Amount of retardation of the select operated groups over the
comparably select normal groups*

CONDITION	PER CENT		
	Trials	Errors	Time
Learning.....	39	34	41
Retention.....	120	400	300
Transfer.....	88	104	84

and hence the learning ability, of the three paired groups whose records are given in tables 11 and 12 thus vary directly with the difficulty of the task. (2) When measured in terms of number of failures, the lesion exerts the greatest effect upon the poorest animals and the least effect upon the superior rats (table 8). Presumably the retarding effect of a lesion also varies inversely with ability.

We thus suggest that the comparative data of table 12 may be explained in terms of the differential effect of the lesion on differences in learning ability, rather than on differences in the difficulty of the task.

If this suggestion is not tenable, and we accept the data in table 12 at their face value, we are forced to conclude that the percentage of retardation is a function of the difficulty of the task.

In this case we have the apparently paradoxical conclusion that the effect of the lesion on *number of failures* varies directly with the difficulty of the task, while its retarding effect on the *successful rats* varies inversely with difficulty. Such a conclusion would at least support the hypothesis of a qualitative distinction in the effect of the lesion upon the two groups of rats.

SUMMARY

In this experiment we compared the effects of a cerebral lesion, approximately constant in size (mean = 18.8 ± 0.38) and locus and shape, on learning, retention, and transfer. Two 12 unit multiple-T mazes of different pattern but of approximately equal difficulty were employed. The six groups were selected in a chance manner resulting in approximately equal initial learning ability.

1. Following this type of lesion, many animals failed to meet the criterion of mastery. The splitting of the operated groups into successes and failures appears to be an "all or none" phenomenon, and it indicates the presence of a distinct qualitative difference in performance in all three of the test conditions. Our data disprove Maier's (5, 6) conclusion that maze learning and reasoning are different and distinct mental operations in that failures are present in one and absent in the other.

2. The number of failures was found to vary directly with the difficulty of the task. Forty-two per cent were eliminated in the learning situation, 28 per cent in transfer, and only 16 per cent in the relearning condition.

3. An important factor determining the success or failure of the animals was found to be the level of maze learning ability. The poorer learners were the more susceptible to the effects of the lesion. The two groups differed but slightly in respect to lesion size, and these variations can not be regarded as an important selective factor.

4. Our preliminary experiments suggest the presence of a critical lesion area, below which there is no retardation and above which the animals fail to learn this particular type of maze.

5. When the normal animals were roughly equated to their

operated comparison group with regard to the selective factor, the retardation was found to vary inversely with the average learning ability of the paired groups, and also with the difficulty of the task.

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